



# Fish thermal habitat current use and simulation of thermal habitat availability in lakes of the Argentine Patagonian Andes under climate change scenarios RCP 4.5 and RCP 8.5



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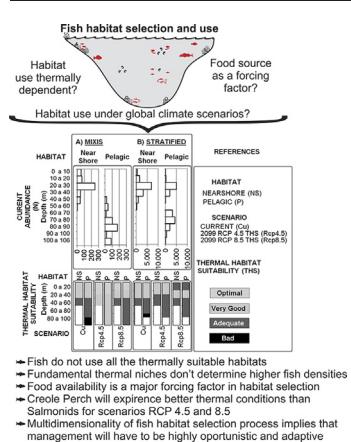
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## HIGHLIGHTS

- Fish do not use the best thermally suitable habitats currently available to them.
- Higher fish densities are not constrained to their fundamental thermal niches.
- Food availability is a major forcing factor in fish habitat selection and use.
- Creole perch will probably benefit from warmer waters due to climate change.
- Salmonids will probably retract from small size shallow lakes and nearshore waters.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Habitat use in relation to the thermal habitat availability and food source as a forcing factor on habitat selection and use of *Percichthys trucha* (Creole perch), *Oncorhynchus mykiss* (rainbow trout), *Salmo trutta* (brown trout) and *Salvelinus fontinalis* (brook trout) were determined as well as future potential thermal habitat availability for these species under climate change scenarios Representative Concentration Pathways 4.5 and 8.5. This study was conducted in three interconnected lakes of Northern Patagonia (Moreno Lake system). Data on fish abundance was obtained through gill netting and hydroacoustics, and thermal profiles and fish thermal habitat suitability index curves were used to identify current species-specific thermal habitat use. Surface air temperatures from the (NEX GDDP) database for RCP scenarios 4.5 and 8.5 were used to model monthly average temperatures of the water column up to the year 2099 for all three lakes, and to determine potential future habitat availability. In addition, data on fish diet were used to determine whether food could act as a forcing factor in current habitat selection. The four species examined do not use all the thermally suitable habitats currently available to them in the three lakes, and higher fish densities are not necessarily constrained to their "fundamental thermal niches" sensu Magnuson et al. (1979), as extensive use is made of less suitable habitats. This is apparently brought about by food availability acting as a major forcing factor in habitat selection and use. Uncertainties related to the multidimensionality inherent to habitat selection and climate change imply that fish resource

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management in Patagonia will not be feasible through traditional incremental policies and strategic adjustments based on short-term predictions, but will have to become highly opportunistic and adaptive.

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## 1. Introduction

It is now widely accepted that the atmospheric accumulation of greenhouse gases such as CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O, HFCs, PFCs, SF<sub>6</sub>, CO and VOCs due to anthropogenic activities leads to global climate warming (Schneider, 1989; Meinshausen et al., 2011; Smith et al., 2011). It is also acknowledged that climate change represents one of the major threats to biodiversity in the near future on global, regional and local scales, with 15–37% of terrestrial species and up to 75% of fish riverine species possibly becoming extinct (Thomas et al., 2004; Xenopoulos et al., 2005). Furthermore, one must also take into account that “predictions indicate that global climate change will continue even if greenhouse gas emissions decrease or cease” (Ficke et al., 2007). In relation to inland water fish, it is widely acknowledged that climate change, whether acting as a direct or indirect driver, is and will be responsible for a variety of responses, ranging from the individual level (Whitney et al., 2016), to populations, assemblages and aquatic communities (Lynch et al., 2016). So far, the identified responses of inland fishes include changes in abundance, growth and recruitment, shifts in migration timing, hybridization, novel species interactions and shifts in species distributions (Lynch et al., 2016). Shifts in species spatial distributions due to temperature change are considered among the most dramatic responses documented on continental, regional and local scales (Alofs et al., 2014; Babaluk et al., 2000; Comte et al., 2013; Comte and Grenouillet, 2013; Eby et al., 2014; Heino et al., 2009; Johnson and Evan, 1990; Lynch et al., 2016). So far, it is generally accepted that warm water species will increase their present distributional ranges as air temperature continues to rise over the years, whereas cold water species will experience a decrease in their distributional ranges.

Although one may anticipate that climate change on continental and regional scales may induce expansion or contraction of a species range, it is much more difficult to foretell what consequences climate change will have on a local scale in terms of habitat use. Until now, most work on lake habitat use and global warming has dealt with the Northern hemisphere, and is related to shifts in the extent of available habitat within the thermal niche of particular species (Jansen and Hesslein, 2004; Magnuson et al., 1990; Cline et al., 2013). However, habitat selection and use is a multidimensional process that involves species preferences in relation not only to physico-chemical water characteristics but also to food and cover availability. Since fish exhibit temperature-dependent selection, preferred temperatures being at or close to the physiological optimum (Coutant, 1987; Tonn, 1990), it has been hypothesized that in any given water body, provided that food is available and competition for resources is not too high, higher species densities will occur in habitats within their thermal niches (Rudstam and Magnuson, 1985). Magnuson et al. (1979) defined the “fundamental thermal niche” as  $\pm 2^{\circ}\text{C}$  of the median preferred temperature, but warned that under field conditions fish may occupy lower temperatures. In lentic water bodies local climate conditions determine thermal structure, and therefore for any given species, thermal habitat availability (Magnuson et al., 1979). However, as explained earlier, habitat use will also be dependent on other drivers such as reproduction, competition, and food and refuge availability. Consequently, even if we can easily measure the amount of suitable available thermal habitat for any given species according to its temperature preferences, this does not imply current thermal habitat use.

In Argentina, most published work considers generalizations regarding overall temperature effects, and consequently possible overall changes in fish distribution. Gonçalves et al. (2010) wrote a comprehensive review on the effects of ultra violet radiation and temperature-

related climate change on both plankton and fishes of freshwater systems in temperate zones. These authors pointed out that “in the Southern Hemisphere, we should distinguish between species limited in their southward distribution by low temperatures and those limited in their northward distribution by high temperatures”. In fact, they also provided evidence suggesting that fish fauna of Neotropical origin has in recent years extended its distribution into Andean and Patagonian ichthiogeographical provinces (“sensu” Lopez et al., 2008) and argue that introduced salmonids in Patagonia will be adversely affected by climate change, whereas the native *Percichthys trucha* (Creole perch) will benefit. Becker et al. (2017) give a comprehensive analysis of the historical biogeography of Patagonian freshwater ichthyofauna that allows for better understanding of present adaptations and associated physiological ecology.

The two best-documented cases for Argentina explore the distribution of *Odontesthes bonaerensis* (silverside bonaerense) (Gomez et al., 2004; Gomez and Menni, 2005) and the distribution of native fish and salmonids in Patagonia (Aigo et al., 2008, 2014; Aigo, 2010). Silverside bonaerense populations have recently experienced an increase in numbers and expansion to formerly dry areas, now flooded due to increased precipitation runoffs, which allows greater connectivity and new habitat availability. In the second case, starting with Aigo et al. (2008), several authors have stated that in Patagonian lakes the relative abundance of native perch has seen an increase, whereas that of salmonids has experienced a significant decline. They have also proposed that salmonids have been excluded from the littoral zone of lakes due to an increase in water temperatures at the lake shores (Aigo et al., 2008; Aigo, 2010).

In Argentine Patagonia, in addition to future global climate changes, managers must deal with a complex scenario where two main management imperatives exist in relation to freshwater fish fauna. One is related to the conservation goals of the National Park System and Non-Governmental Conservation organizations, and the other is fostered by local, regional and national governments associated with development and enhancement of the economic movement based on salmonid sport fisheries (Rechencq et al., 2017). This has led to a “development vs conservation management debate” which has been documented by several authors (Cussac et al., 2016; Macchi and Vigliano, 2014; Pascual et al., 2009; Rechencq et al., 2017; Vigliano and Alonso, 2007), who all agree that this “debate” has hindered rather than helped current, sound, management practices. In addition to this complex scenario, there are other threats to the goals of both these management imperatives: the introgression of new exotics from Chilean aquaculture, damming, and urban development (Habit et al., 2010). These stressors, more often than not, act synergistically on a local or regional scale (Cussac et al., 2016; Macchi and Vigliano, 2014; Pascual et al., 2009; Vigliano and Alonso, 2007). Therefore, management of the fresh water fish fauna of continental Patagonia has to be viewed as a multidimensional problem extending over multiple spatial, temporal, biological and sociological scales, and influenced by climate change. Successful future management in relation to conservation goals or economic development of sport fisheries requires, among other things, knowledge of the influence of other forcing factors on current thermal habitat use. This would allow better understanding of possible future changes in habitat use due to climate warming.

Within this context, the goals of this paper are to investigate current fish habitat use in relation to thermal habitat availability and food source as a forcing factor in habitat selection as well as to model future thermal habitat availability under different climate change scenarios. Partial objectives of the present paper are: 1) to evaluate, for three Patagonian lakes, present habitat use by adults of the four top fish

predators found in the system, and to determine the relationship between habitat selection, thermal habitat availability and source habitat of food items, and 2) to simulate potential shifts in thermal habitat availability for all four species by the end of the century under climate change scenarios RCP 4.5 and RCP 8.5.

## 2. Material and methods

### 2.1. Study area

The study was conducted in the Moreno Lake System, which is formed by three interconnected, morphologically different water bodies located in the Northern Patagonian Andean Range (Fig. 1). Two of the water bodies, Moreno Este and Moreno Oeste, are warm monomictic deep oligotrophic transparent lakes of glacial origin, whereas the third is a shallow lake with lower transparency. Morphological and limnological characteristics (Table 1) were taken from the literature (Morris et al., 1995; Probst and Eckmann, 2009; Rechencq et al., 2011), measured with an YSI multiparameter sonde or estimated following standard procedures (Wetzel and Likens, 1991), and were found to be similar to those of other lakes in Chile and Argentina. Although the surface areas of lakes Moreno Este and Moreno Oeste are similar ( $\approx 6 \text{ km}^2$  each), other morphological and limnological characteristics differ (Table 1), providing differential habitat type availability. The trophic webs in this system are similar to that of other Patagonian Andean Lakes that present low species diversity (Macchi et al., 2007; Pascual et al., 2007; Modenutti et al., 2010). Only eight fish species are commonly found in these lakes. The most abundant species is a native forage fish, the small puyen (*Galaxias maculatus*), which is a key prey species in Patagonian Andean lakes (Juncos, 2012; Juncos et al., 2013; Rechencq et al., 2014). The second most abundant is *Percichthys trucha* (creole perch), followed by *Oncorhynchus mykiss* (rainbow trout), *Salmo trutta* (brown trout), *Salvelinus fontinalis* (brook trout), big puyen (*Galaxias platei*), the velvet catfish (*Diplomystes viedmensis*) and the Patagonian silverside (*Odontesthes hatcheri*). Creole perch, rainbow, brown and brook trout are the four top predators in the system.

### 2.2. Current species-specific habitat use

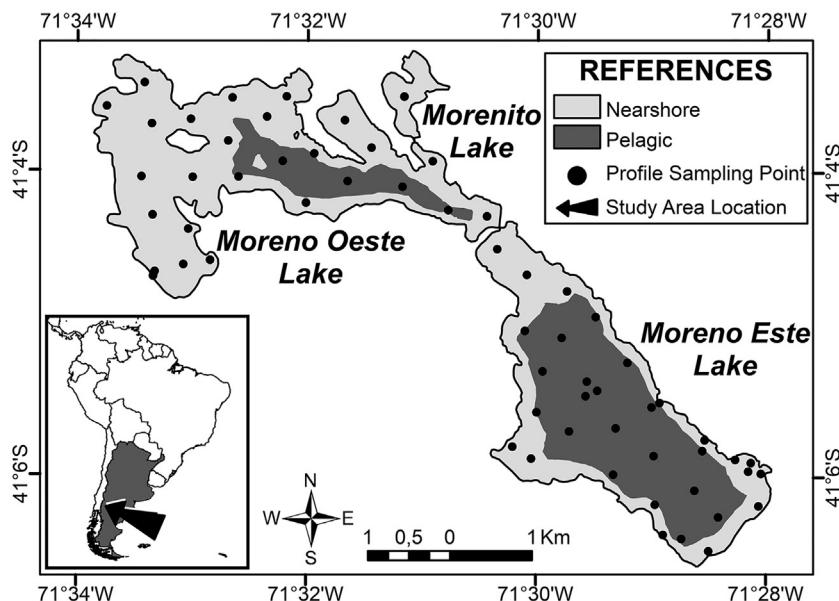
In order to determine current species-specific thermal habitat use by all four top predator species we modified the habitat definitions used in previous studies for this lake system (Rechencq et al., 2011, 2014).

**Table 1**

Morphological and limnological variables of Moreno Lake system. a. Estimated through GIS; b. volume (sensu Wetzel and Likens, 1991); c. from Rechencq et al. (2011); d. Thermocline for Moreno Este and Moreno Oeste ranges from 15 to 20 m in thickness and is usually present from November to April, whereas in Morenito Lake during this period temperature varies gradually from surface to bottom, with no discernible thermocline; e. measured with a multiparameter YSI sonde; f. Kd par (Morris et al., 1995); g. Z1% (sensu Probst and Eckmann, 2009).

| Variables   | Source | Moreno<br>Este | Moreno<br>Oeste | Morenito |
|---|--------|----------------|-----------------|----------|
| Surface área ( $\text{km}^2$ )                      | a      | 6.14           | 6.09            | 0.83     |
| Fetch (km)  | a      | 4.7            | 5.2             | 0.44     |
| Width (km)  | a      | 2.1            | 1.8             | 0.73     |
| Volume ( $\text{hm}^3$ )                            | b      | 424.2          | 208.7           | 5.81     |
| Maximum depth (m)                                   | c      | 106            | 88              | 12       |
| Average depth (m)                                   | c      | 51             | 28              | 5        |
| Mixis average $^{\circ}\text{C}$                    | e      | 7.4            | 6.3             | 7        |
| Stratified average $^{\circ}\text{C}$               | e      | 10.8           | 11.4            | 15       |
| Secchi disk (m)                                     | c      | 16             | 15              | 5        |
| Diffuse attenuation coefficient ( $\text{m}^{-1}$ ) | f      | 0.16           | 0.14            | 0.35     |
| Euphotic Zone depth Z1%                             | g      | 29             | 33              |          |
| Euphotic Volume ( $\text{hm}^3$ )                   | b      | 170.7          | 145.2           | 5.81     |
| Aphotic volume ( $\text{hm}^3$ )                    | b      | 253.5          | 63.6            | 0        |

These authors considered that three different habitats can be found in both Moreno Este and Moreno Oeste. The first, called "Nearshore", comprises both the littoral and open waters where the lake floor lies at a depth of up to 60 m, where light penetration and proximity to the bottom are considered important. The second, defined as "Superficial-pelagic", comprehends the water layers that extend from the surface to 60 m depths where the lake bottom lies at a depth of over 60 m. Light penetration influences this habitat, but it is not in close proximity to the bottom. The third, termed "Deep-pelagic" corresponds to the zone below the previous one, extending from 60 m down to the bottom. In this zone, light is scarce to null, and there is a wide area of contact between the water column and lake bottom. In this study, in order to derive species-specific distributions for both Moreno Este and Moreno Oeste, we considered 10 m depth strata, used the Nearshore habitat as previously defined, and united the Superficial and Deep pelagic habitats into a single Pelagic habitat. Morenito Lake, due to its small size and shallowness, was considered in its entirety as Nearshore habitat. Fish distributions by habitat during the mixis and stratification periods for Moreno Este and Moreno Oeste were derived by re-analyzing data of



**Fig. 1.** Study area: Moreno Lake system. Nearshore and pelagic habitats and thermal profile sampling points.

fish larger than 12 cm total length from previous work during 2007–2008 (Rechencq, 2011; Rechencq et al., 2011, 2014), obtained through 10 m depth stratified gillnetting and hydroacoustic samplings. For Morenito Lake, fish distribution was derived from bibliographic data (Aigo, 2010) and unpublished catch and hydroacoustic data of our research group.

### 2.3. Thermal structure of the lakes

Current thermal structure during mixis and stratified periods was determined for all three lakes using a YSI V2 multiparameter sonde. In order to determine whether Nearshore (i.e. near shore waters with coastline on 2 or <2 sides), closed bays (i.e. those near shore waters with coastline on three sides), and open waters of Moreno Este and Moreno Oeste have varying thermal structures, 58 thermal profiles of both mixis and stratification periods were analyzed (Fig. 1). Due to the small size and shallowness of Morenito Lake it was considered in its entirety as Nearshore habitat, and therefore only one thermal profile for mixis and stratification periods was recorded.

### 2.4. Suitable thermal habitat availability

As ectotherms, fish maintain thermal homeostasis through behavioral mechanisms, mostly related to avoidance of unsuitable temperatures. Provided that there are no other drivers at work (e.g. feeding, reproduction, predator avoidance.) they remain in waters within their thermal operational range and as close as possible to operational thermal optimums. Therefore, in order to best represent the thermal suitability and availability of habitats in the lakes we divided the water column into 10 m depth strata, and defined the thermal suitability of each one according to species-specific thermal operational optimums and ranges, and the temperature suitability index curves (SI). These are simple mathematical representations of habitat quality as a function of temperature for juvenile and adult stages of the species of interest. Curves range from 0 (worst) to 1 (best) possible habitat conditions and allow delimitation of temperature ranges which correspond to differing thermal habitat suitability in relation to the thermal operational range of each species. For salmonids we used existing SI curves (Raleigh, 1982; Raleigh et al., 1984, 1986; Newcomb et al., 2007). For Creole perch we developed a temperature SI curve from biological, distributional and temperature preference data (Aigo et al., 2014; Amalfi, 2009; Baigun and Ferriz, 2003; Liotta, 2006). For the range of temperatures covered by each species SI curve, we defined four possible habitat conditions or types (Table 2), which were cross checked in relation to bibliographical thermal preferences and current thermal distributional ranges. Thus we defined: a) Optimal: the range of temperatures with SI values of 1, b) Very Good: the range of temperatures with SI values between 0.99 and 0.75, C) Adequate: the range of temperatures with SI values between 0.749 and 0.4 and d) Bad: the range of temperatures with SI values lower than 0.4.

**Table 2**

Species-specific thermal habitat suitability limits based on T°C Suitability Index (SI) curves.

| SI category   | Optimal | Very good          | Adequate          | Bad   |
|---|---------|--------------------|-------------------|-------|
| SI range values   | 1       | 0.99–0.75          | 0.749–0.4         | <0.4  |
| Species specific temperature (T°C) range for each SI category |         |                    |                   |       |
| Creole perch  | 20–23   | >14 < 20/24 < 25.5 | >8 < 14/25.5 < 27 | <8/27 |
| Rainbow trout   | 12–18   | >7 < 12/18 < 21    | >3 < 7/20 < 23    | <3/23 |
| Brook trout   | 10–16   | >6 < 10/16 < 19.5  | >3 < 6/19.5 < 22  | <3/22 |
| Brown trout   | 12–19   | >9–12/19 < 21      | >5 < 9/21 < 24    | <5/24 |

### 2.5. Simulation of potential species-specific available thermal habitats under RCP 4.5 and RCP 8.5 scenarios

To analyze possible shifts in habitat availability due to climate change, we developed, tested and fitted several simple models in order to predict possible surface and at-depth water temperature changes in relation to air surface temperatures. Initial variables tested for the models were chosen according to the perceived importance in determining water temperatures. Thus monthly mean surface air temperatures, wind velocities and direction, mean maximum monthly surface air temperature, mean monthly water temperatures at 10 m depth intervals were used to construct and test varying models. Data to fit the models came from field measurements in the lakes, as well as from the INTA meteorological database (Bariloche) for years 1996–2003. After an initial model construction, we discarded wind velocities and direction as variables for the models because it is currently not possible to predict with any accuracy wind velocities and direction farther than a few days ahead. Mean monthly surface air temperature was also discarded as variable because models show better fit and prediction when mean maximum monthly surface air temperatures are used. For lakes Moreno Este and Moreno Oeste, best fit was obtained through a multiple regression model that estimated average monthly surface (0–10 m) water temperature (MASW 0–10 m T°C month n) according to the equation:

$$\text{MASW}_{0-10} \text{T}^\circ \text{C}_n = a + b * \text{MASW}_j \text{T}^\circ \text{C}_{n-1} + c * \text{MASA T}^\circ \text{C}_n$$

where a, b and c are constants,  $\text{MASW}_{0-10} \text{T}^\circ \text{C}_{n-1}$  is the mean water temperature in the 0–10 m depth strata for the previous month and  $\text{MASA T}^\circ \text{C}_n$  is the mean maximum surface air temperature for month n.

We then fitted a simple linear regression model to estimate the monthly average temperature of successively deeper 10 m water layers or strata (J-1) from the average monthly water temperature of the strata immediately above it (J).

$$\text{MAWT}^\circ \text{C}_{(J-1)} = a + b * \text{MAWT}^\circ \text{C}_J$$

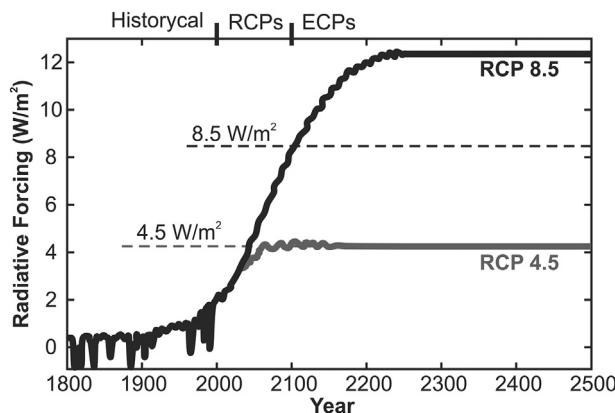
where a and b are constants and  $\text{MAWT}^\circ \text{C}_{(J-1)}$  is the mean water temperature of the deeper strata and  $\text{MAWT}^\circ \text{C}_J$  the mean average water temperature of the shallower strata.

For Morenito Lake, possibly because of its shallow depth and small size, the best fit was given by:

$$\text{MASW}_{0-10} \text{m T}^\circ \text{C month}_n = a + b * \text{MAAir T}^\circ \text{C month}_n$$

where  $\text{MASW}_{0-10} \text{m T}^\circ \text{C month}_n$  is the mean water temperature in the 0–10 m depth strata for the month, a, b are constants and  $\text{MAAir T}^\circ \text{C month}_n$  is the mean maximum air temperature for the month.

These models were used to predict possible surface and at-depth water temperature changes in relation to air surface temperatures up to the year 2099, under Representative Concentration Pathways 4.5 and 8.5 (RCP 4.5 and RCP 8.5) scenarios. These two scenarios were chosen for comparison purposes because they are considered to respectively be the most probable and extreme outcomes of current global climate change trends. We also decided to run simulation up to the year 2099 because by that year RCP 4.5 will have stabilized (Fig. 2). These RCPs are two of the multi-gas emission scenario trajectories adopted by the Intergovernmental Panel on Climate Change for its fifth Assessment Report in 2014 (IPCC-AR5, 2014), which correspond to the possible radiative forcing values of +4.5 and +8.5 W/m<sup>2</sup> in the year 2100, relative to pre-industrial values. These two scenarios imply estimated increases in mean air temperatures of 1.8 °C (probable range 1.1 to 2.6 °C) and 3.7 °C (probable range 2.6 to 4.8 °C), respectively (Moss et al., 2007). While RCP 4.5 contemplates an increase in



**Fig. 2.** The Representative Concentration Pathways (RCP) 4.5 and RCP 8.5 modified from Meinshausen et al. (2011).

greenhouse gases (GHG) up to the year 2100 when concentration levels off, RCP 8.5 contemplates a continuous increase of GHGs into the XXIII century (Fig. 2).

In order to predict average water temperatures for all depth strata of the three studied lakes, the fitted models were run from November 2007 to November 2099. Average maximum air temperature for each month used as input to the models for the simulated period was calculated from the "Surface air Temperatures NASA Earth Exchange Global Daily Downscaled Projections" database (NEX-GDDP, 2018). This database provides simulated maximum temperature daily projections for the RCP 4.5 and RCP 8.5 scenarios across the entire globe, with a spatial resolution of  $0.25^\circ \times 0.25^\circ$ . Daily maximum temperature values from the grid square closest to the INTA meteorological station were used to calculate projected average monthly maximum air temperatures which were used as primary inputs to the models.

## 2.6. Species specific feeding source habitat

In order to determine whether feeding could be a forcing factor conditioning current habitat use by fish in all three water bodies, we analyzed fish stomach content data of all four fish species for each lake, assigning to each prey item found its probable source habitat, defined according to its life history trait characteristics as benthonic or open waters. We then estimated the seasonal percentual distribution by habitat of provenance of the diet, by species, lake and season.

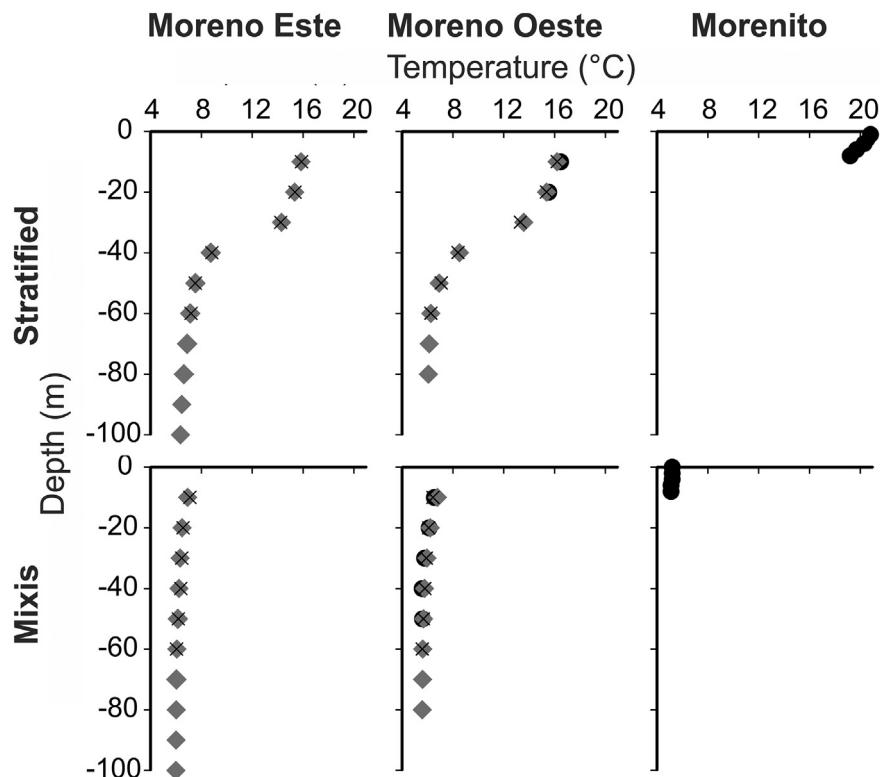
## 3. Results

### 3.1. Present thermal structure of the lakes

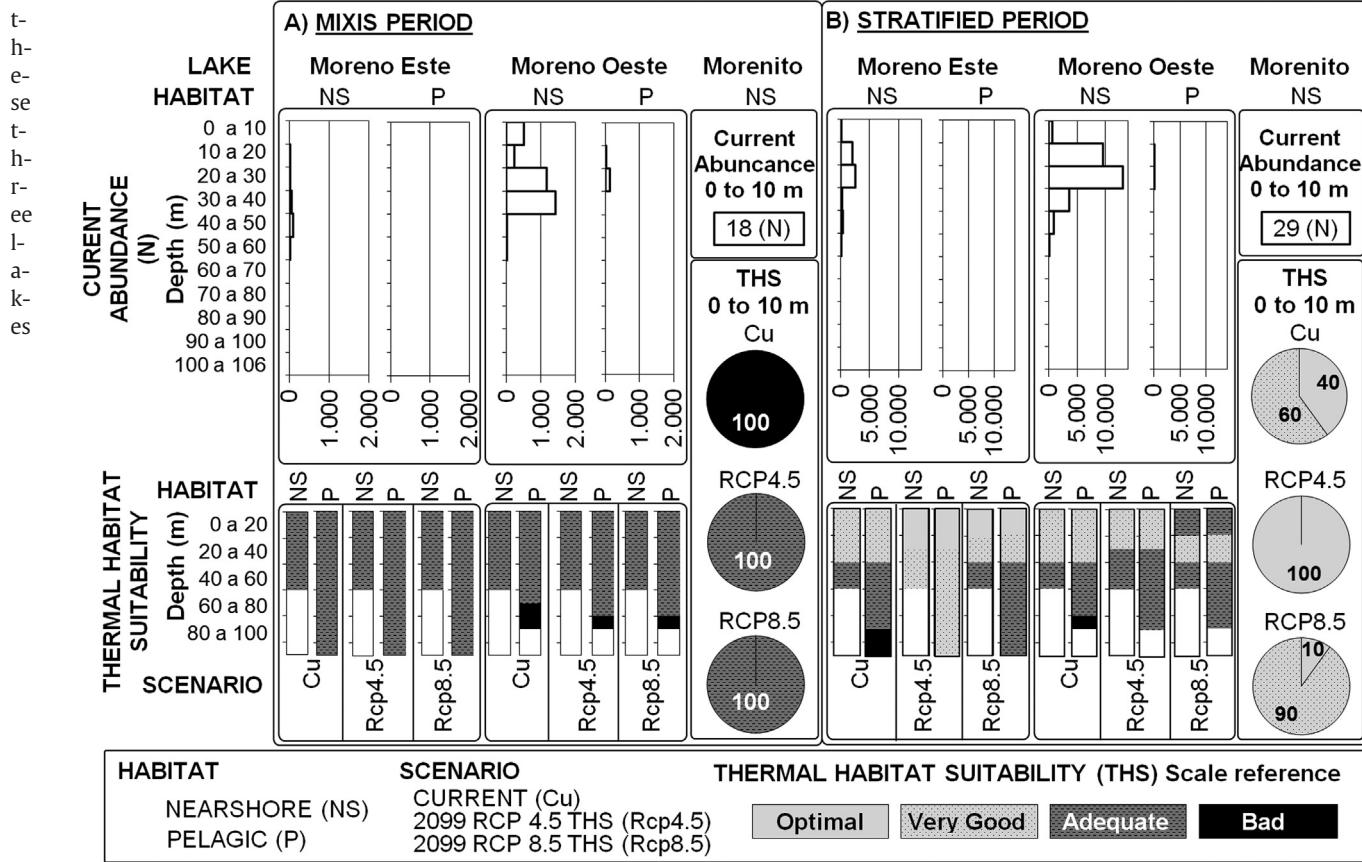
According to the analysis of thermal profiles, mixis and stratified periods were well defined for all three lakes. Temperature profile analysis of both Moreno Este and Moreno Oeste Lakes also showed that regardless of lake mixis or stratification, temperature differences between bay areas, nearshore and open waters for any given depth never exceeded 0.5 °C. Since this does not imply a shift in terms of the habitat suitability ranges used in this study, and can also be considered of no biological significance, the nearshore and upper strata of the pelagic thermal habitats were considered identical (Fig. 3). During mixis the surface and bottom temperatures of both Moreno Este and Moreno Oeste lakes ranged between 6 and 7 °C, whereas the water temperature in Lake Morenito ranged between 5 °C and 8 °C throughout the water column. During stratification, lakes Moreno Este and Moreno Oeste showed sharp decreases of 6 and 8 °C between 20 and 45 m depths, respectively, and Morenito lake showed a 2 °C drop between 3 and 8 m depths, ranging between 11 and 16 °C.

### 3.2. Present thermal habitat use by the four studied species

The four freshwater fish species considered in this study do not utilize all of the thermally suitable habitats currently available to them in



**Fig. 3.** Temperature depth profiles by lake for stratified and mixis periods, for ● closed bays, ◇ nearshore and \* open waters (superimposed values may hide symbols).



**Fig. 4.** a, b. Creole perch present abundance and current suitable thermal habitat (Current THS) availability by lake, mixis period (a) and stratification period (b), and depth, and potential thermal habitat availability for 2099 under RCPs 4.5 (2099 RCP 4.5 THS) and 8.5 (2099 RCP 8.5 THS) scenarios for Moreno Este, Moreno Oeste, and Morenito lakes. Histograms reflect present fish abundance. Habitat thermal suitability scale: ■ Optimal, ■■ Very Good, ■■■ Adequate, ■■■■ Bad. Numbers within pie graphs represent percentage of overall lake availability of each thermal habitat suitability.

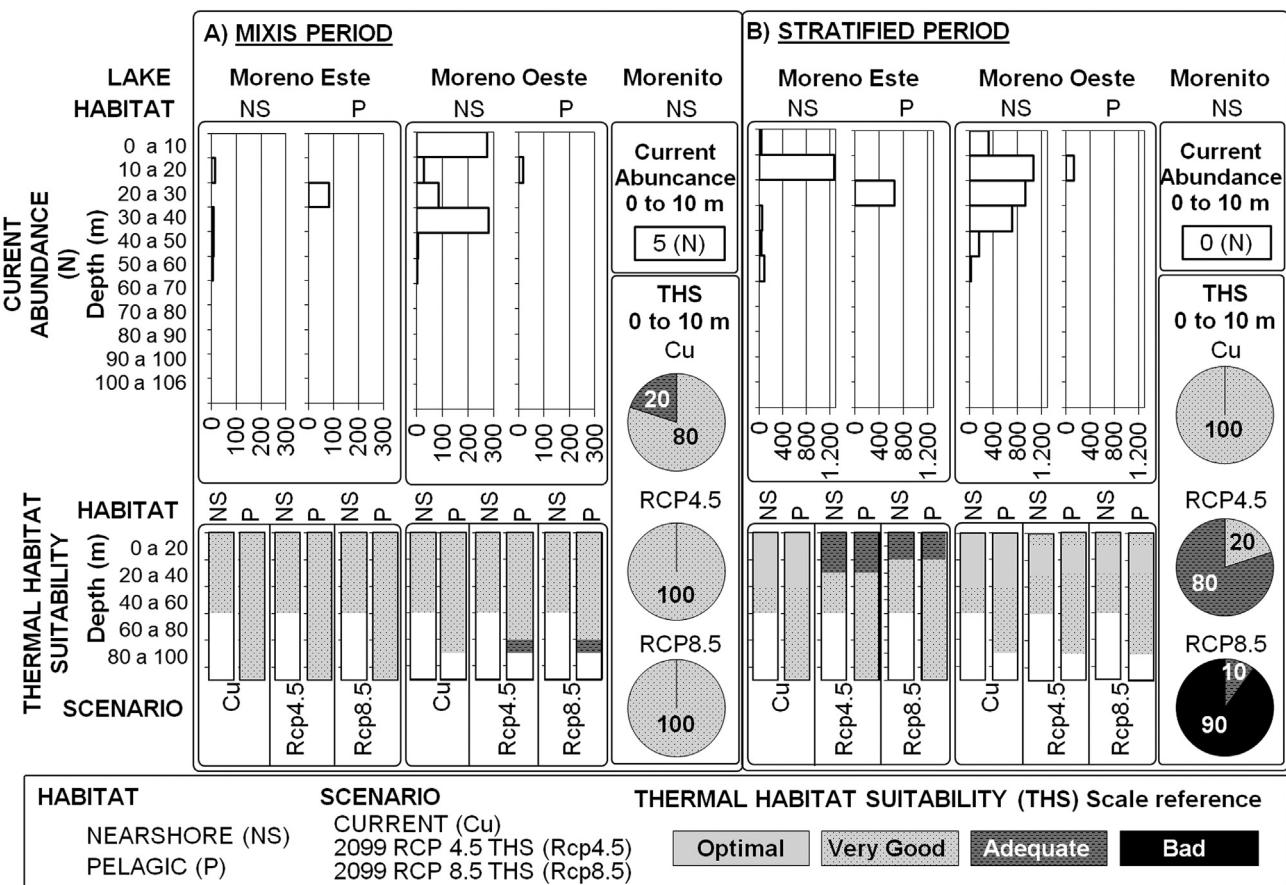
(Figs. 4–7), and higher fish densities are not necessarily constrained to their “fundamental thermal niches” sensu Magnuson et al. (1979). Catch and hydroacoustic data show that there is extensive use of the nearshore habitat (0–60 m depths) by all species, despite, in some cases, that this habitat presents merely thermally “Adequate” conditions, such as for Creole perch and brook trout during mixis in both Moreno Este and Moreno Oeste lakes (Fig. 4a–b). In contrast, there is restricted use of the upper strata of the Pelagic zone by rainbow and brown trout and null use of the deeper strata by all four species (Figs. 4a–b–7a–b). Apparently, only Creole perch use Morenito Lake continuously, despite the fact that for all salmonid species it also presented some suitable thermal habitat throughout the year.

Analysis of probable thermal habitat availability for each studied species in all 3 lakes under scenarios RCP 4.5 and 8.5 for the year 2099 revealed that thermal suitability patterns vary between lakes (Figs. 4–7). These differences are probably due to the thermal requirements of each species, and differences in lake morphometry (i.e. shape of basin, wind, shoreline development, wave action and depth), which condition their thermal structure. Morenito Lake showed the biggest shift in habitat suitability, presumably because its small size, shallowness and highly vegetated waters contribute to its warming under both RCP scenarios. Despite the fact that under both RCP scenarios water temperature would increase, during mixis habitats in all three lakes would remain invariant or would show a slight tendency towards improvement in thermal suitability for all species. However, during stratification shifts, available suitable thermal habitats must be considered on a species-by-species basis. Thus, Creole Perch would benefit from both global warming scenarios during stratification in all lakes, due to increased thermal suitability of the used habitats (Fig. 4a–b).

For salmonids (Figs. 5–7) the picture is more complex, the overall tendency being a decrease in habitat suitability during stratification. A major decrease in the suitability of currently used habitat for the 3 salmonids would occur mainly in Morenito Lake, followed by Moreno Este and to a lesser extent by Moreno Oeste Lake. Brook trout is the species with the worst prognosis, with some of the currently used habitats attaining “Bad” suitability conditions.

### 3.3. Feeding as a forcing factor in habitat selection

The fact that the studied species are not currently using all thermally suitable available habitats indicates that there are other forcing factors at play in relation to habitat selection and use. Our results regarding the probable habitat of origin of food items found in stomach contents indicate that perch, regardless of lake and period, feed almost entirely nearshore benthonic organisms (78–96%), such as insect larvae, *Samastacus* sp. and *Aegla* sp., with a small percentage of puyen chico (Table 3). Whereas salmonids feed on a higher proportion of organisms found in open waters of both the nearshore and superficial strata of the Pelagic habitat. Rainbow trout stomach contents showed the most varied diet, consuming in both Moreno Este and Moreno Oeste a higher proportion of organisms found in open waters (97% - 51% respectively) such as other fish and terrestrial insects. The most-consumed open water prey in both lakes and periods was the small puyen. Benthonic diet items were predominantly decapods of the genus *Samastacus* sp. and *Aegla* sp. as well as *Anisoptera* larvae. No food items were found in stomachs of fish caught in Morenito Lake. Brook trout in both Moreno Este and Moreno Oeste fed mostly on open water organisms (54–94% respectively) except during Mixis of Moreno Oeste, when all stomachs



**Fig. 5.** a, b. Rainbow trout present abundance and current suitable thermal habitat (Current THS) availability by lake, mixis period (a), stratification period (b) and depth, and potential thermal habitat availability for 2099 under RCPs 4.5 (2099 RCP 4.5 THS) and 8.5 (2099 RCP 8.5 THS) scenarios for Moreno Este, Moreno Oeste, and Morenito lakes. Histograms reflect present fish abundance. Habitat thermal suitability scale: ■ Optimal, ■■ Very Good, ■■■ Adequate, ■■■■ Bad. Numbers within pie graphs represent percentage of overall lake availability of each thermal habitat suitability.

analyzed showed 100% organisms of benthonic origin. Open water diet items were once again mostly small puyen, salmonids and terrestrial insects, whereas those of benthonic origin were Chilina sp., Samastacus sp. and Aegla sp. Brown trout stomach content analysis showed that only those specimens caught in Moreno Oeste had stomach contents, which corresponded entirely to fish (i.e. small puyen and perch, the latter being the most abundant) (Table 3).

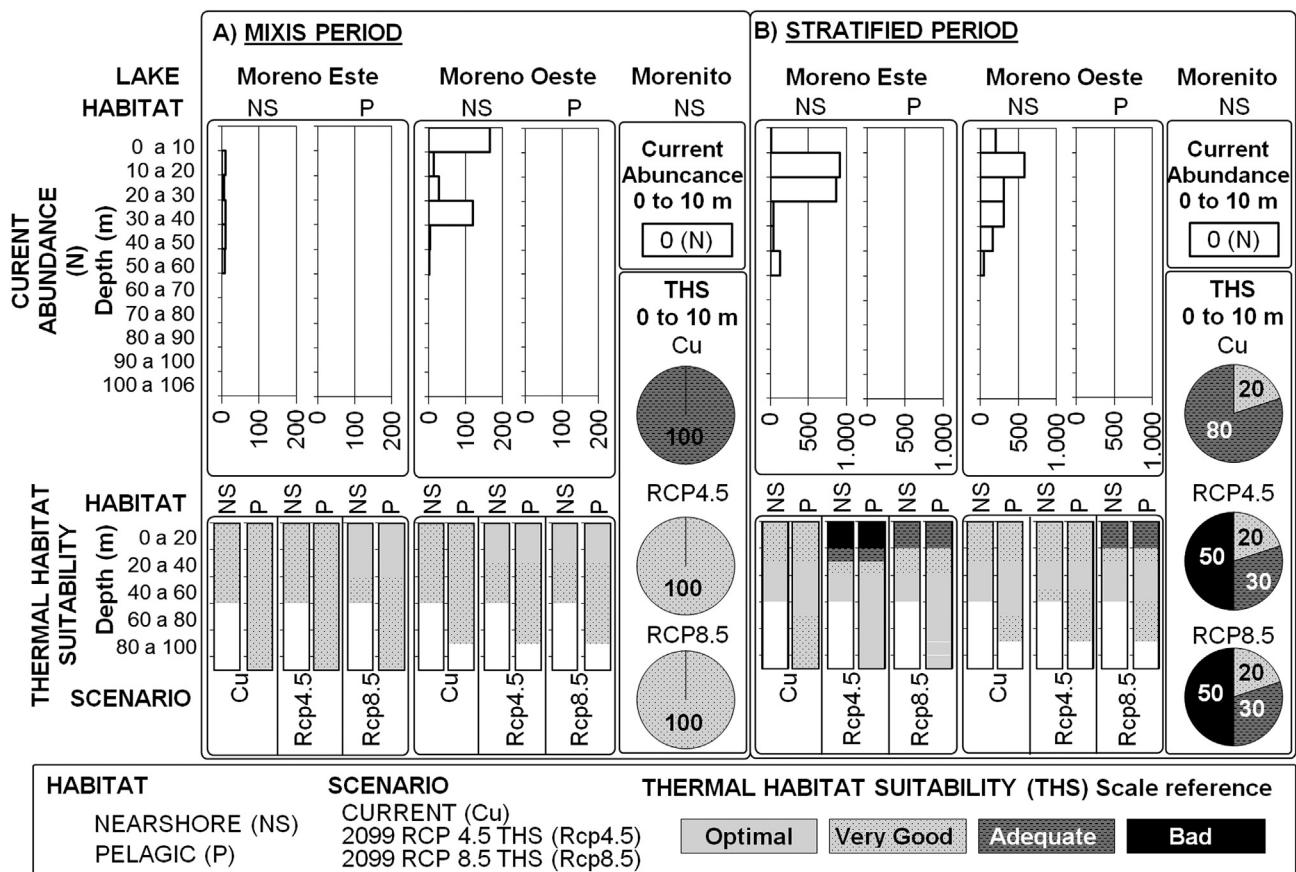
#### 4. Discussion

Our results coincide partially with those of Aigo et al. (2008), Cussac et al. (2009) Aigo (2010) and Aigo et al. (2014) in relation to overall better thermal conditions for Creole perch, and the fact that salmonids will be most severely affected in small shallow lakes such as Morenito Lake, where deep thermal refugia are nonexistent. These authors also state that in deep lakes salmonid withdrawal from the littoral zone should be expected, and has according to them supposedly already occurred. However, the littoral zone as they define it actually encompasses only the shallow littoral habitat (i.e. 0–5 m), this being the area most influenced by winds, wave action, aquatic vegetation, shoreline development and lake morphometry. Therefore, it is probable that high temperatures will be experienced only where the shallow littoral has protection from these factors, implying that the overall importance of salmonid withdrawal from the shallow littoral zone in any particular lake will depend on lake morphometry and the amount of protected coastline. Concerning the deeper strata of closed bays, near shore and open waters, our thermal profile field data showed no current significant differences between these lake sectors. This implies that shifts in thermal suitability would affect them in similar ways. According to

thermal suitability models, the current most heavily used depth strata (i.e. below 5 m depths) of the nearshore habitat under both RCP scenarios would retain varying viable conditions on a species-by-species basis.

Our results regarding the probable habitat of origin of food items found in stomach contents indicate that food is a major forcing factor in relation to habitat selection and use. Thus, perch feed mostly on benthonic organisms, whereas salmonids feed on a higher proportion of organisms found in open waters. Previous work has shown that all four species undergo ontogenetic diet shifts, the prey consumed varying from smaller to bigger sizes as consumer size increases (Juncos et al., 2015). This shift also implies a change in the proportions of the source habitat of food eaten. Thus, the earlier life stages of all four species tend to consume mostly insect larvae and benthonic organisms of small size. Upon reaching a certain size, creole perch tends to incorporate more benthonic macrocrustaceans (i.e. Samastacus sp. and Aegla sp.) than rainbow or brook trout. These species also tend to incorporate more open water organisms (i.e. fish such as small puyen, salmonids and Creole perch). Brown trout diet has been shown to be the most piscivorous of all four species, although it does consume large quantities of Samastacus sp. (Vigliano et al., 2009; Juncos, 2012, this paper).

One particular aspect to be analyzed is the apparent absence of all four studied fish species from the deeper strata of the pelagic habitat (i.e. >60 m depths) of both Moreno Este and Moreno Oeste lakes, despite suitable thermal conditions and availability of potential prey. Previous studies have shown that below 60 m depths huge numbers of Galaxiid larvae congregate during daylight hours, forming dense sound scattering layers (i.e.  $1 \times 10^9$  larvae per km $^2$ ) at depths of 100 m (Lindegren et al., 2012; Rechencq et al., 2011, 2014, 2017), and also that important numbers of big puyen adults can be found at even



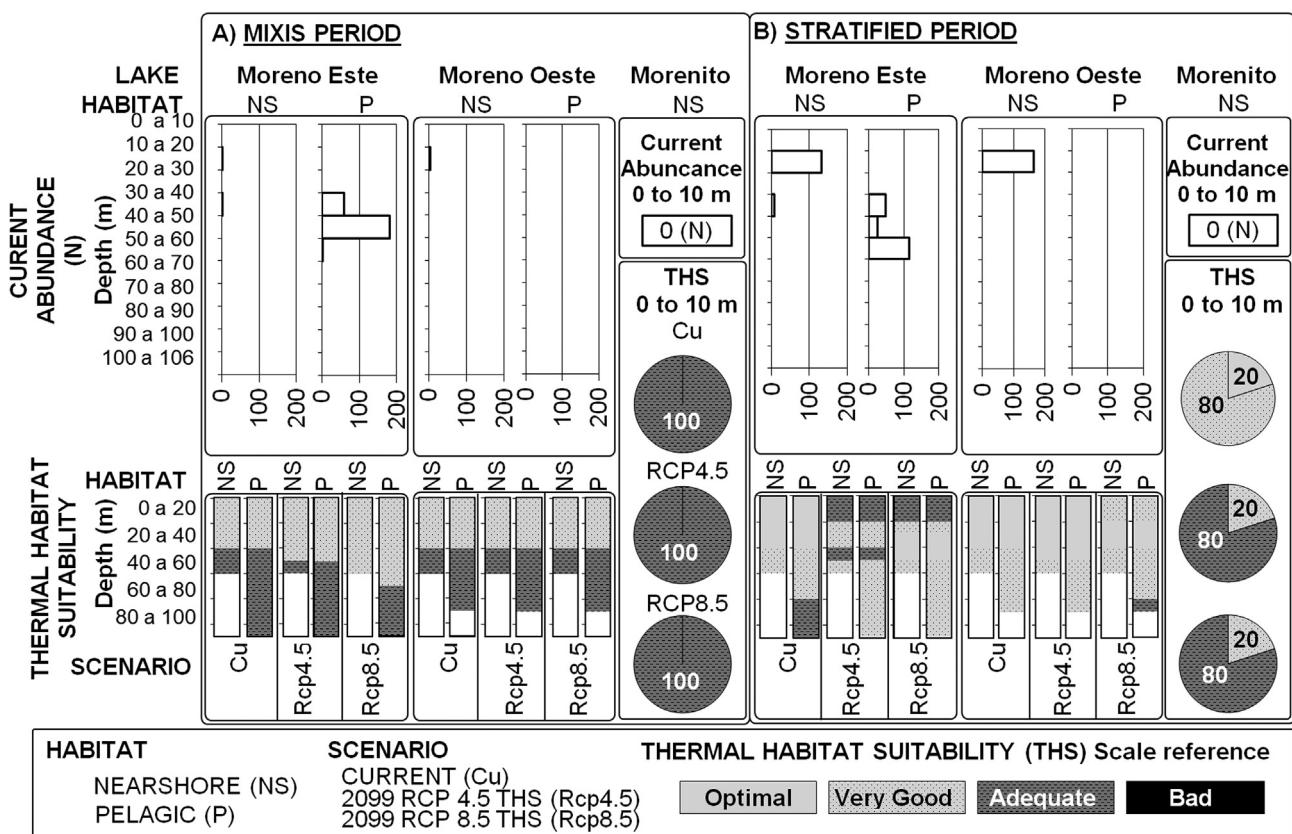
**Fig. 6.** a, b. Brook trout present abundance and current suitable thermal habitat (Current THS) availability by lake, mixis period (a), stratification period (b) and depth, and potential thermal habitat availability for 2099 under RCPs 4.5 (2099 RCP 4.5 THS) and 8.5 (2099 RCP 8.5 THS) scenarios for Moreno Este, Moreno Oeste, and Morenito lakes. Histograms reflect present fish abundance. Habitat thermal suitability scale: ■ Optimal, ▨ Very Good, ▨ Adequate, ■ Bad. Numbers within pie graphs represent percentage of overall lake availability of each thermal habitat suitability.

greater depths. While the latter species is well adapted to the lack of light at such depths and can readily feed on small puyen larvae (Milano, 2003), salmonids and Creole perch are visual predators, thus it is likely that they cannot find prey available to them in the deeper portions of both lakes. *Samastacus* sp., a benthonic dweller that has been recorded at 250 m depths at the bottom of regional lakes (our group, unpublished data) would also be unavailable to the four fish species being considered, due to lack of light. Thus, we conclude that the current low numbers of adults of the four species studied in this paper in the upper strata of pelagic waters, despite suitable thermal conditions, can be attributed to low prey density in comparison with the Nearshore habitat. In contrast, their complete absence in the deeper strata of the pelagic zone, despite suitable thermal habitat conditions, can be attributed to insufficient light levels for feeding on the overly abundant Galaxiid larvae and/or the adult big puyen inhabiting these waters. The lack of salmonids in Morenito Lake cannot be attributed to lack of light, due to its shallowness and transparency. However, food availability to predators may be hindered because of the shallow bottom, and the highly abundant submerged and emergent vegetation of this mesotrophic lake serves as a refuge to invertebrates and small puyen juveniles and adults.

In view of the thermal habitat use, feeding habits and prey distribution explained above, we conclude that while temperature may influence habitat selection and use by fishes in North Andean Patagonian lakes, food availability is a major forcing factor in the process. Thus future actual habitat selection and use will not depend only of available thermal habitats but more so of the synergic availability of thermal habitats and food in relation to species specific life histories and strategies. Thus, retraction by salmonids from the lakes shallow littoral (i.e. 1–5 m)

as has been proposed (Aigo et al., 2008, 2014; Cussac et al., 2009; Aigo, 2010) should not proof detrimental as long as there are enough deeper thermal refugia with enough food resources. This is in accordance with the Rudstam and Magnuson (1985) hypothesis that in any given water body higher fish densities will be found within their thermal niche as long as food is available. This implies that thermal tolerance, actual thermal habitat use and prey preferences should be taken into account in any future studies on global warming effects upon fish populations. Furthermore, since habitat selection is a multidimensional process, and other factors such as lake morphometry, reproductive drives and predation avoidance can be at play, the predictive capabilities of studies that consider only changes on thermal habitat are limited.

Management of the fish resources of continental Patagonia has to be viewed as a multidimensional problem subject to the actual effects of climate change. Management of freshwater fish resources in Argentina is mostly carried out by national and provincial agencies through incremental policies and strategy adjustments based on short-term questions and predictions. Healey (1990), studying the implications of climate change for fishery management policies, states that this type of approach and the usual responses in terms of prevention, mitigation and adaptation are not suitable for addressing climate change effects, due to the associated uncertainties. This author concludes that policy adjustments are likely to be defensive and mitigative, whereas they should be opportunistic and adaptive. So far, in Northern Patagonia, climate change effects would seem to benefit the conservation imperative related to the native perch, and be detrimental in an unknown measure to the economic development imperative based on introduced salmonid sport fisheries. Thus, whether climate change can be seen as good in terms of controlling the exotics or bad in term of sport-fishery



**Fig. 7.** a, b. Brown trout present abundance and current suitable thermal habitats (Current THS) availability by lake, mixis period (a), stratification period (b), and depth, and potential thermal habitat availability for 2099 under RCPs 4.5 (2099 RCP 4.5 THS) and 8.5 (2099 RCP 8.5 THS) scenarios for Moreno Este, Moreno Oeste, and Morenito lakes. Histograms reflect present fish abundance. Habitat thermal suitability scale: ■ Optimal, ▨ Very Good, ▨ Adequate, ▨ Bad. Numbers within pie graphs represent percentage of overall lake availability of each thermal habitat suitability.

development is only a matter of perceptions and choice of the different stakeholder groups involved and therefore becoming part of the ongoing development vs conservation management debate. Hence, unpredictability associated with inherent uncertainties, as well as the human factor appear to indicate that fish resource management in Patagonia would have to become highly opportunistic and adaptive.

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Table 3

Table 3  
Percentual source of food diet items found in the stomach contents of fish caught, by species, lake and period.

| Species              | Creole Perch |            |              |            |          |            | Rainbow trout |            |              |            | Brook trout |            |              |            | Brown trout  |
|----------------------|--------------|------------|--------------|------------|----------|------------|---------------|------------|--------------|------------|-------------|------------|--------------|------------|--------------|
| Lake                 | Moreno Este  |            | Moreno Oeste |            | Morenito |            | Moreno Este   |            | Moreno Oeste |            | Moreno Este |            | Moreno Oeste |            | Moreno Oeste |
| Period               | Mixis        | Stratified | Mixis        | Stratified | Mixis    | Stratified | Mixis         | Stratified | Mixis        | Stratified | Mixis       | Stratified | Mixis        | Stratified | Stratified   |
| <b>Food resource</b> |              |            |              |            |          |            |               |            |              |            |             |            |              |            |              |
| Diet item            |              |            |              |            |          |            |               |            |              |            |             |            |              |            |              |
| <b>Benthonic</b>     |              |            |              |            |          |            |               |            |              |            |             |            |              |            |              |
| Amphipoda            |              |            | 36.8         | 0.0        |          | 22.4       | 0.4           |            | 0.0          | 0.1        |             |            |              |            |              |
| Chironomid larvae    |              |            | 8.3          | 0.1        |          | 14.1       | 61.1          |            |              |            |             |            |              |            |              |
| Chironomid pupae     |              |            |              |            |          |            |               |            |              | 0.1        |             |            |              |            |              |
| Chilina              |              |            |              |            |          |            |               |            | 9.1          | 1.0        |             |            |              |            |              |
| Samastacus           | 61.0         |            | 20.7         | 48.7       |          |            |               |            |              |            | 19.4        |            |              |            |              |
| Aegla                | 1.5          |            |              | 3.5        |          |            |               |            | 10.7         |            | 10.5        |            |              |            |              |
| Ephemeroptera larvae |              |            |              |            |          |            | 0.1           |            | 0.2          | 0.4        | 0.5         |            |              |            |              |
| Tricoptera larvae    |              |            |              |            |          |            | 1.1           |            | 0.9          |            | 7.8         |            |              |            |              |
| Zygoptera larvae     |              |            |              |            |          |            |               |            |              |            | 0.5         |            |              |            |              |
| Hirudinea            |              |            |              |            | 15.7     |            |               |            |              |            |             |            |              |            |              |
| Anisoptera larvae    | 90.8         | 19.1       | 29.6         | 40.3       | 25.8     | 33.5       | 3.8           | 0.5        | 10.5         | 1.3        | 0.8         | 2.2        | 23.9         | 0.4        |              |
| <b>Open waters</b>   |              |            |              |            |          |            |               |            |              |            |             |            |              |            |              |
| Adult insects        |              |            |              |            |          |            | 1.1           |            | 4.5          |            | 1.9         | 6.6        |              | 0.2        |              |
| Small puyen          | 9.1          | 18.3       | 4.6          | 7.4        | 22.0     | 2.7        | 63.3          | 93.5       | 51.4         | 84.9       | 97.3        | 9.8        | 93.4         | 8.2        |              |
| Salmonids            |              |            |              |            |          |            | 6.7           |            |              |            |             | 38.3       |              |            |              |
| Perch                |              |            |              |            |          |            | 5.4           |            |              |            |             |            |              |            | 91.8         |
| Benthonic total      | 90.8         | 81.7       | 95.4         | 92.6       | 78.0     | 96.2       | 24.7          | 2.1        | 48.6         | 15.1       | 0.8         | 45.4       | 100.0        | 6.4        |              |
| Open water total     | 9.1          | 18.3       | 4.6          | 7.4        | 22.0     | 3.8        | 75.3          | 97.9       | 51.4         | 84.9       | 99.2        | 54.6       | 0.0          | 93.6       | 100.0        |

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